

The effects of habitat fragmentation on the reproduction and abundance of *Angadenia berteroi*

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Abstract

Aims

The pine rocklands of southern Florida are a fire-dependent forest associated with outcrops of limestone. Pine rockland plants have several adaptations to fire, and for many species, burning increases plant growth, flowering and seedling establishment. The pine rockland forest has been reduced and fragmented in recent decades. Outside of Everglades National Park, only 2% of the original pine rocklands remain, and they are in the form of small fragments. Our objective is to investigate the effects of fragmentation and habitat quality on abundance and plant reproductive fitness of *Angadenia berteroi* (A.D.C.) Miers, a threatened species of the southern Florida pine rockland.

Methods

We estimated the density of plants using a stratified random sampling design, and reproductive fitness (in terms of percentage of plants with flowers and fruit) by walking transects in an array of habitat fragments of different sizes and degrees of isolation (distance

to the nearest fragment) as well as in continuous habitat. Structural equation modeling (SEM) was employed to investigate how *A. berteroi* reproductive fitness was affected by fragmentation and habitat quality.

Important Findings

Habitat fragment size was correlated with the density of *A. berteroi*, but did not have a great impact on its reproductive success. However, habitat quality represented by litter depth and subcanopy cover had strong negative effects on the reproductive fitness of *A. berteroi*, suggesting that increased light availability and low litter cover resulting from recent fires may favor reproduction.

Key words: habitat fragmentation, habitat quality, isolation, fire, structural equation modeling, reproductive fitness, abundance

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INTRODUCTION

Habitat destruction and fragmentation are the principal causes of biodiversity loss. Habitat fragmentation affects the reproductive biology of a species (Yates and Ladd 2005), and can reduce species richness as well as genetic variability (the diversity of genotypes and alleles present in species or populations) (Vargas *et al.* 2006). For plants, reduction in genetic variability affects pollen quality and seed production (Aspinwall and Christian 1992; Vargas *et al.* 2006). Usually, there is reduced gene flow among plants in the remnant fragments compared with those in intact habitat (Aizen and Feinsinger 1994; Young *et al.* 1996). Thus, reductions in genetic variability may also increase the population's extinction risk through inbreeding

depression, ultimately diminishing the population's ability to respond to environmental disturbances (Frankham 2005). The genetic consequences of habitat fragmentation may result in fitness decline and increase the isolation of populations occupying the remaining fragments, consequently causing reduced population size in the fragments (Frankham 2005; Young *et al.* 1996), and ultimately affecting seed germination or seedling fitness due to the effects of inbreeding depression and lower genetic diversity caused by fragmentation (Honnay and Jacquemyn 2007). Low population sizes can result in Allee effects, defined as positive (inverse) density dependence at low densities, where the fitness of individuals is lower than expected (Courchamp *et al.* 1999). However, for some herbs, habitat fragmentation does not affect the abundance of the

species, probably because the plants can disperse among fragments, or the fragments are larger than the minimum critical size for population maintenance (O'Brien 1998).

Both habitat destruction and fragmentation may modify ecological interactions between species, such as pollination and herbivory (Laurence 2002). Insect-pollinated plants may be at a disadvantage in fragmented habitats, because the size of fragments, as well as the distance between fragments, may have effects on the distribution and abundance of insect species (Artz and Waddington 2006). Additionally, plants in fragmented populations may exhibit reduced population density with reduced floral display and rewards that can result in fewer pollinations. Pollen quality may also decrease at low plant densities due to matings between siblings or other related individuals; pollen can also be wasted as a result of self-incompatibility mechanisms in self-incompatibles species (Coombs et al. 2009; Lamont et al. 1993; Levin et al. 2009).

The pine rockland ecosystem is unique in the United States and is considered an imperiled habitat (Koptur 2006). Pine rockland flora is a mixture of tropical and temperate taxa, with a very diverse understory (Snyder et al. 1990; US Fish and Wildlife Service 1999). Many of the more than 200 understory species are endemic, some are threatened and some are rare. The high levels of endemism in pine rockland ecosystems may be explained by the presence of unique limestone outcrops and calcareous, phosphorus-limited soils. The calcium-rich loams and high pH, along with the presence of iron and manganese, contrast with the acidic quartz sand found in pine forests of northern Florida (O'Brien 1998).

Landscapes where pine forests were once dominant have experienced dramatic human population growth over the last 100 years, leading to much destruction of pine rockland habitat. Outside of Everglades National Park, only 2% of the original pine rocklands remain in many small fragments (Koptur 2006; Snyder et al. 1990). The remaining pine rockland habitats are threatened because they are primarily fire maintained systems, but pineland fragments embedded within the urban landscape are not burned as frequently as they once were. Within two decades of fire exclusion, a pine rockland can become a closed-canopy subtropical dry forest (known as 'hardwood hammock'), resulting in the disappearance of pine trees and rich native herbaceous flora (Snyder et al. 1990). In addition, the accumulation of litter due to fire suppression adversely affects understory species richness and diversity (Kirkman et al. 2001). In this ecosystem, leaf litter represents a physical barrier to plant growth and inhibits seed germination and establishment (Hiers et al. 2007; Wendelberger and Maschinski 2009). Litter modifies the physical and chemical environment of the forest floor, affecting soil moisture and nutrient availability (Hiers et al. 2007) that ultimately influences the distribution and abundance of understory species in the pine forests.

Angadenia berteroi (A.DC.) Miers (Apocynaceae, Apocynoideae) is a tropical perennial subshrub with large yellow flowers; its distribution is south Florida, the Bahamas

and Cuba. In southern Florida, *A. berteroi* grows in the pine rocklands, rockland hammocks and marl prairies in Miami Dade and Monroe Counties (Gann et al. 2002; Wunderlin and Hansen 2011). This threatened perennial plant is more abundant in the largest pine rockland fragments with higher fire frequency (Barrios et al. 2011). *A. berteroi* flowers open before sunrise and last less than 12 h. The flowers have complex floral morphology (Barrios and Koptur 2011) that results in a specialized pollination system (Barrios et al. 2016). Fruit set from self-pollination is unlikely to occur because the species is predominantly self-incompatible (Barrios and Koptur 2011). Natural levels of fruit set in *A. berteroi* are low, probably due to low visitation by pollinators, mating between closely related individuals, or both (Barrios and Koptur 2011).

The widespread distribution of *A. berteroi*, nearly ubiquitous in pine rockland sites, makes it an ideal species to study how fragmentation affects the reproductive fitness of a pollinator-dependent native species. The objective of this research is to establish the effect of habitat fragmentation and habitat quality on abundance and plant reproductive fitness of *A. berteroi*. Since fragmentation can adversely affect the diversity and abundance of insect pollinators (Artz and Waddington 2006), we hypothesized that contiguous large tracts of habitat are more favorable for *A. berteroi*, and that both the reproductive success and fitness of the species will be positively correlated with the size of the forest fragment. Fragmentation is also linked to habitat quality. We hypothesized that deterioration of habitat quality resulting from the suppression of fires will have a negative impact on the reproductive success and fitness of *A. berteroi*. We assessed the influence of fragmentation and habitat quality, and their interactions with various factors affecting seedling density, flowering and fruit set, using structural equation modeling (SEM), a multivariate statistical approach that allows the evaluation of interactions among different variables (Grace 2006). The hypothetical model for the causal relationships among these factors is given in Fig. 1. We also used an experimental approach to evaluate the effect of habitat size on seedling emergence and vigor.

MATERIALS AND METHODS

Study sites

We measured reproductive traits of *A. berteroi* and its habitat variables in 13 pine rockland forest sites scattered along the Miami Rock Ridge, including fire management units within Everglades National Park (ENP) (Table 1). Study sites were chosen based on their size and degree of isolation from the continuous pine rocklands in ENP (Fig. 2; Table 1).

Habitat structure and fragmentation

Fragment size, fire history and distance to the nearest fragment for fire management units within the Park and the Miami-Dade County fragments were determined using the Fire History Geodatabase provided by Everglades National Park (ENP), and the geographic information system (GIS)

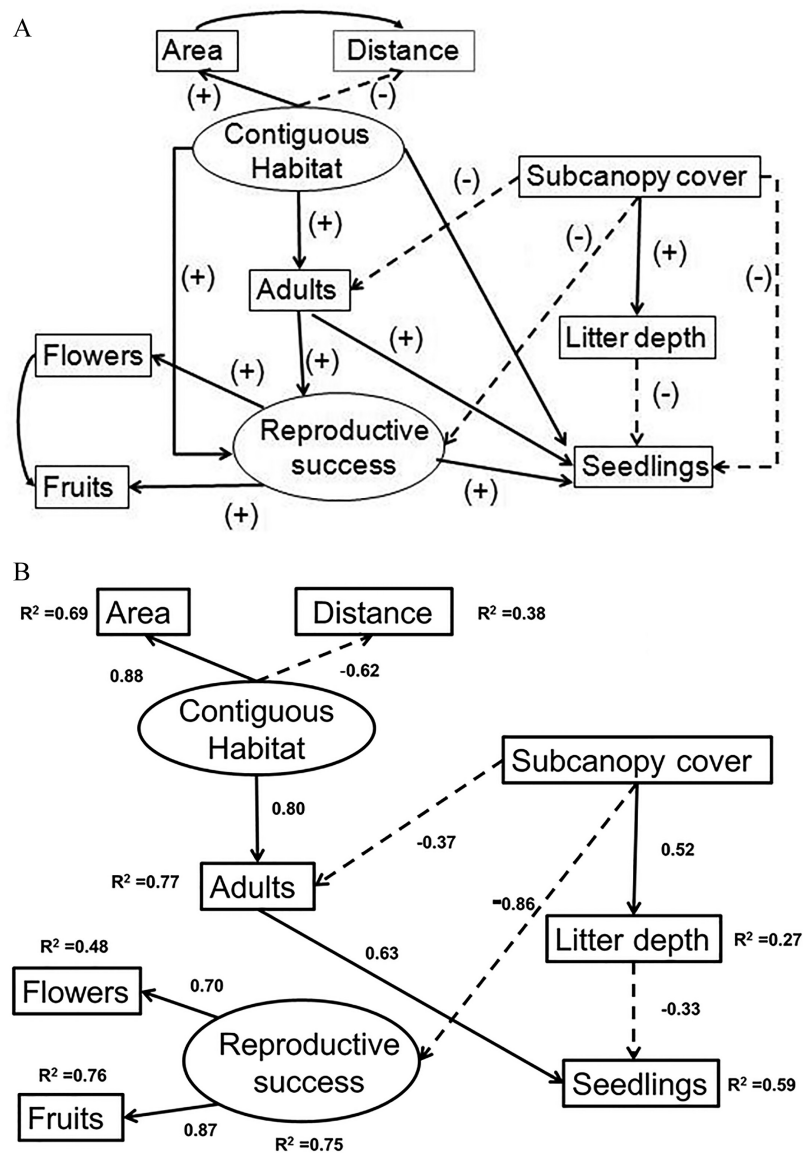


Figure 1: structural equation model illustrating the interactions between habitat fragmentation and quality with the reproductive fitness of *Angadenia berteroi*. Single arrows indicate directional relationships between the variables. Solid lines represent positive relationships and dashed lines represent negative relationships. (A) A priori basic model including all the variables and the potential relationships among them. (B) Actual model indicating significant relationships. Numerals near each path indicate standardized regression coefficient. Oval boxes are latent variables and square boxes are observed variables.

data generated by Florida Natural Areas Inventory (Public Lands-June 2008 shape files), respectively. Distance to the nearest fragment was determined as point-to-point linear distance between the centers of each fragment using ArcGIS version 10.0 (ESRI Inc.). We measured both litter depth and subcanopy closure, as both are considered representative of habitat quality, microhabitat structure and physical indicators of fire return interval, and both increase with time since the last fire (Snyder *et al.* 1990). Litter depth was measured with a rigid wire and a rule scale to the nearest 0.5 cm at three points across the plot diameter within each plot. Subcanopy closure was estimated by counting the number of squares of a forestry spherical densiometer occupied by canopy image excluding

pine trees. The densiometer readings were taken in four cardinal directions from the center of each plot at a height of 0.5 m, respectively.

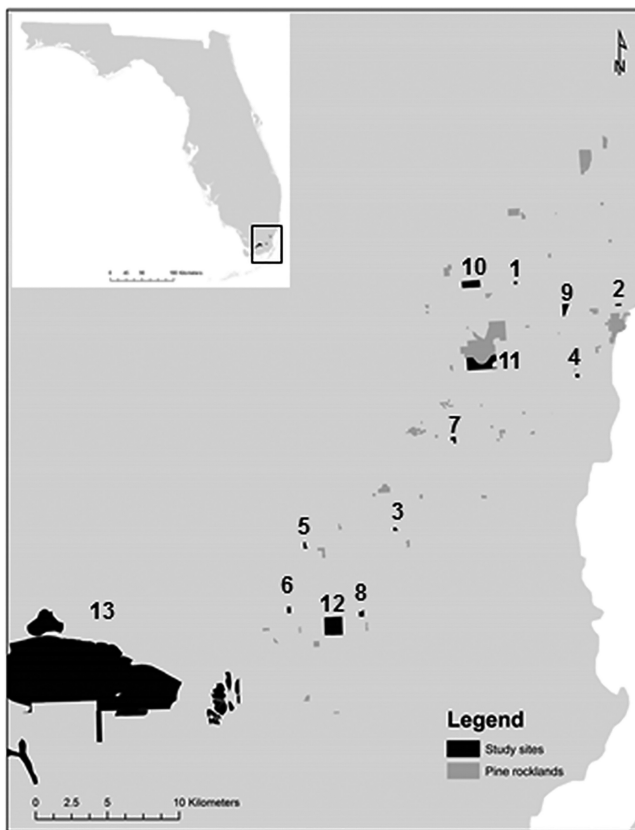
Fragmentation, abundance and reproductive fitness

We used a stratified random sampling design to quantify the density of *A. berteroi*. At each site, one to six 30×30 m blocks were selected, avoiding edges of the sites, and to ensure that 5% of the site was surveyed. In each block, we sampled 10, 1-m radius circular random plots. In each plot, we recorded the number of adults and seedlings of *A. berteroi*. Each separate aerial stem was considered a separate individual, and we

Table 1: Pine rockland study sites in Miami-Dade County, Florida, used for *Angadenia berteroi* study

Site names	Site number	Area (Acres)	Distance to nearest fragment (km)
Pine Shore Preserve	1	7.8	2.09
Ludlam Pineland	2	10.2	0.9
Ingraham Pineland	3	10.4	1.34
Ned Glenn Nature Preserve	4	11.0	0.43
West Biscayne Pineland	5	15.1	1.01
Palm Drive Pineland	6	20.0	1.59
Silver Palms Groves	7	20.4	1.22
Florida City Pineland	8	23.5	0.96
Rockdale Pineland	9	37.1	1.83
Nixon Smiley Pineland Preserve	10	120.0	1.2
Larry and Penny Thompson Park	11	270.0	0
Navy Wells Pineland	12	353.2	1.44
Long Pine Key	13	12 322.2	0

Site names, number designation, area and distance to the nearest fragment (as figured from central points).

**Figure 2:** map of the pine rockland habitat in southern Florida. Study sites shown here are described in Table 1.

defined seedling as individuals ≤ 10 cm in height and adults as individuals > 10 cm in height. We then calculated the density of adults and seedlings as individuals per m^2 .

To examine the effect of fragmentation on reproductive fitness, we determined the number of plants with flowers and fruits and the density of seedlings within each fragment. Two observers surveyed, by walking for 2 h at each site during the flowering peak in May, counting the total number of adult plants. To ensure that sampling distance covered by both observers in 2 h was the same, their walking speed was tested and was not found significantly different. The number of flowers per plant was recorded for each individual. We repeated these measurements in June during peak fruiting (Barrios et al. 2011), when we recorded the total number of plants and the number of fruits per plant. The percentage of flowering and fruiting plants was estimated by dividing the number of flowering and fruiting plants by the total number plants counted. The mean percentage of plants with flowers and fruits was used to estimate reproductive success of *A. berteroi* at each site. Both reproductive success and seedling density were used to estimate the reproductive fitness of *A. berteroi* (see online supplementary Appendices).

Statistical analysis

Our goal was to investigate the effect of habitat fragmentation on reproductive output using an integrative approach. For this, we used structural equation modelling (SEM) to explore the direct and indirect effect of predictors on response variables, taking into account the causal effects among variables (Grace 2006; Grace et al. 2014). SEM models represent network hypotheses and typically involve multiple regression equations. The SEM analysis starts by building an analytical model representing all the hypothetical causal links between predictors and response variables, based on previous studies of the ecological system. We sought to evaluate the direct and indirect effects of landscape variables (fragment size and distance to the nearest fragment) and site quality variables (litter depth and subcanopy closure) on *A. berteroi* density (adult and seedling) and reproductive output (percentage of individual plants with flowers and fruit) at the site level (Fig. 1A). For this analysis, adults and seedling density as well as the reproductive measurements and the habitat quality parameters were averaged for each of the 13 sites. The SEM Model includes two latent variables: habitat fragmentation and reproductive success. Habitat fragmentation was estimated in this model as a function of two measured variables: area of the fragment and point to point distance to the center of the nearest fragment. Reproductive success was measured in this model as a function of the mean percentage of plants with flowers and fruits.

We conducted a SEM analysis in R version 3.1.2 (R Core Team 2012) using the Lavaan package, 'latent variable analysis' (Rosseel 2012). Direct effects were measured by standardized regression coefficients between the predictor and response variables, while the indirect effects were calculated as the sum of the products of all standardized regression coefficients over all paths between the predictor and the response variables. The maximum likelihood chi-square value was

used to estimate the fit of model, and the final model was chosen on the basis of the Akaike Information Criterion (AIC) (Bollen *et al.* 2014). A non-significant goodness of fit test indicated that there is no significant discrepancy between model and data. Since our design considered each site as an experimental sample in order to accurately characterize landscape processes, our sample size was small ($N = 13$). We also tested the goodness of fit by Haughton's BIC test (HBIC) (Bollen *et al.* 2014). Prior to analysis, square root transformations were performed to achieve normality if the data were not normally distributed.

Seedling emergence and vigor

At least five mature fruits from seven sites (Sites 2, 3, 8, 10, 11, 12 and 13) were collected. Seed mass (an indicator of seed quality) and offspring fitness (seedling germination and survivorship) were calculated for each site. Each seed was weighed to the nearest 0.1 mg, and the mean seed mass of 15–20 seeds per fruit was calculated for each fruit. From each site, a total of 330 seeds were weighed. Later, seeds within each site were mixed to eliminate genetic differentiation among fruits and 274 seeds per site were planted in six-pack trays, one seed per cell. The trays were placed on a mist bench for 2 weeks. Seed trays were moved to the greenhouse at the end of the second week, and we counted the number of seedlings present 3 weeks after planting. Seedling emergence was measured as the total number of seedlings that emerged by week 3, expressed as a percentage of the total number of seed sown. Seedling vigor was estimated from plant height at weeks 5 and 9 (Kearns and Inouye 1993). Percentage of seedlings present and plant height was compared across the different sites.

To see whether seed mass had an effect on germination success, we collected at least five mature fruits per site from five sites (sites 9, 10, 11, 12 and 13). Weighed seeds (573 in total) were soaked for 5 min in 5% bleach solution to sterilize the seeds, and were then rinsed thoroughly with distilled water. Seeds were placed in well plates that were filled with distilled water, with one seed per well. Five replicates were performed per site and 12 seeds per replicate were used. The seeds were germinated in a growth chamber at 25°C, 60% humidity, in a 12 h/12 h light/dark regime. We monitored seed germination daily for 2 weeks.

Statistical analysis

Data were checked for normality and equal variances before conducting statistical analyses. Analysis of variance (ANOVA) was used to test for differences among sites for seed mass, percentage of seedlings present and plant height, as data were normally distributed. Post hoc tests were conducted using Tukey HSD (Honestly Significant Difference) to test for differences among sites. We performed correlation analyses using Spearman's coefficient to investigate the relationship between seed mass and germination success, and between seedling size with fragment size (Green and Salkind 2007; Zar 1999). Statistical analyses were performed using SPSS

(Statistical Package for the Social Sciences) version 21 (SPSS 2014).

RESULTS

Fragmentation, abundance and reproductive fitness

The structural equation model (Fig. 1B) containing all significant relationships found in the multiple regression analyses showed a good fit between the model and the data ($\chi^2_{17} = 15.05$, $P = 0.592$).

The SEM model revealed that adult density was significantly affected by habitat fragmentation and subcanopy cover. The area of a fragment had a positive effect on adult density, while distance to the nearest fragment and subcanopy cover had negative impact on adult density (Fig. 1B). Seedling density was directly and positively affected by adult density, and negatively by litter depth. As expected, subcanopy cover had positive effects on litter depth. Neither habitat fragmentation nor subcanopy cover had direct effects on seedling density. However, both habitat fragmentation and subcanopy cover had an indirect effect on seedling density, primarily through adult density and litter depth, respectively. Reproductive success, represented by number of plants with flowers and fruits, was negatively influenced by subcanopy cover, but we found no significant relationship between either fragmentation or adult density and reproductive success (Fig. 1B).

Seedling emergence and vigor

Seed weight differed significantly among sites ($F_{6, 330} = 27.88$, $P < 0.0001$, Table 2). Sites 2 and 13 had heavier seeds, while sites 10 and 3 had lighter seeds (Table 2). Despite those differences, the percentage of seeds producing seedlings in the greenhouse did not differ significantly among sites ($F_{6, 45} = 2.05$, $P = 0.083$). Additionally, seed germination was positively correlated with seed weight ($r = 0.34$, $P < 0.0001$). Seedling height differed significantly among sites at both 5 and 9 weeks ($F_{6, 168} = 8.08$, $P < 0.0001$; $F_{6, 168} = 7.38$, $P < 0.0001$ respectively, Table 2) after planting; furthermore, seedling height was negatively correlated with fragment size ($r = -0.41$, $P < 0.0001$).

DISCUSSION

In fragmented habitat, plant populations are adversely affected by declining habitat quality. In this study, the SEM model indicated that *A. berteroi* does best in large natural areas that are close to other pine rockland sites. Conversely, we also found that *A. berteroi* is less abundant in fragments with high subcanopy cover; an indicator of deteriorated habitat quality. These results are in accordance with our previous studies, where we found *A. berteroi* to be more abundant in larger fragments with higher fire frequency (Barrios *et al.* 2011). Another study (Possley *et al.* 2008) also reported that fragment size had a positive influence on understory species richness, and that *A. berteroi* is one of the species with the

Table 2: mean and standard deviation of seed mass, seedling emergence and plant height

Site	Seed mass (mg)	Seedlings emergence (%)	Height (m) week 5	Height (m) week 9
2	1.24±0.40 ^a	53.70±21.70 ^a	1.24±0.48 ^{ab}	1.88±0.61 ^{ab}
3	0.70±0.34 ^b	62.96±33.10 ^a	1.33±0.60 ^b	2.51±1.33 ^b
8	0.95±0.39 ^c	61.11±53.58 ^a	1.04±0.41 ^{abc}	1.91±0.92 ^{ab}
10	0.57±0.50 ^b	77.78±13.61 ^a	0.91±0.38 ^{ac}	1.65±0.87 ^a
11	0.96±0.33 ^c	41.67±34.56 ^a	0.73±0.23 ^c	1.34±0.41 ^a
12	1.01±0.29 ^c	63.89±34.02 ^a	0.94±0.34 ^c	1.32±0.56 ^a
13	1.30±0.20 ^a	91.67±9.13 ^a	0.75±0.20 ^{ac}	1.46±0.37 ^a

Sites with the same letter are not significantly different with Tukey HSD *post hoc* test.

greatest mean coverage in sites with high fire frequency. Our results also showed seedling density to be negatively correlated with litter depth, and indirectly correlated with subcanopy cover. Increased canopy cover contributes to greater litter development as well as reduces light availability for understory plants (Hiers *et al.* 2007). Increased litter depth and light reduction due to fire suppression alter the physical and chemical properties of the forest floor, and those changes inhibit seedling germination and establishment (Hiers *et al.* 2007; Wendelberger and Maschinski 2009). We found that seedling height was negatively correlated with fragment size; perhaps the tendency of smaller fragments to be overgrown has selected taller seedlings that can grow above the accumulated litter. Some species (e.g.; *Trifolium sp.*, Harrod and Halpern 2005, Harrod and Halpern 2009) have better germination in burned plots due to the removal of the inhibitory effects of litter accumulation, as well as the reduction of competitive plants and increased light availability. Time since the last fire was also negatively correlated with population growth rates of *Chamaecrista keyensis*, endemic herb of the lower Keys pine rocklands, which had reduced density in sites unburned for more than 15 years (Liu *et al.* 2005). Not all species are negatively affected by fragment size or isolation. For instance, herbaceous *Galactia* spp., also endemic to pine rocklands, were not affected by fragment size, though their abundance was negatively affected by plant cover (O'Brien 1998); competition for light, nutrients and space were suggested causes for their diminished abundance in overgrown sites (O'Brien 1998).

Lack of fire in pine rockland fragments may promote the number and growth of exotic species (O'Brien 1998), which play an important role in species composition by affecting seed germination, seedling establishment and occurrence of rare native plants (Yates and Ladd 2005). In many of the remaining pine rockland fragments of southern Florida, the increase in canopy cover is due to the invasion of non-native species (O'Brien 1998; Possley *et al.* 2008). Even though we do not have data to examine the correlation between non-native species and the abundance of *A. berteroi*, the negative correlation between *A. berteroi* density and subcanopy cover suggests that the introduction of exotics also negatively affects the population of this species. In our study, seedling density

at a site was not correlated with the percentage of individual plants with flowers and fruit in the SEM models, contrary to our expectations. This indicates that habitat quality (litter depth and subcanopy cover), which is also related to the time since last fire, plays a strong role in controlling seedling germination and establishment of *A. berteroi*.

We also found *A. berteroi* to be more abundant in less isolated fragments. These results concur with Lienert and Fischer (2003) who reported that both fragment size and isolation have negative effects on the abundance of *Primula farinosa* mainly because of the combined effects of inbreeding depression and lower genetic diversity in more isolated populations. Habitat loss and isolation are consequences of habitat fragmentation (Digiovinazzo *et al.* 2010), where isolation has a negative effect on species richness because it negatively affects migration between fragments. Although we do not have data to examine seed dispersal between fragments, *A. berteroi* seeds are wind dispersed, suggesting that dispersal of seeds to nearby fragments may easily occur (Barrios pers. obs). Bruna (2003) reported that dispersal between nearby fragments can ameliorate the negative effects of fragmentation on population growth rate and reproduction. More work on this aspect is needed, especially on the possibility of long distance dispersal with extreme weather events such as hurricanes.

Contrary to our expectation, we found no significant relationship between reproductive success and either adult density or fragmentation. Other studies have also shown that reproduction is unaffected by fragmentation (Bruna and Kress 2002; Yates and Ladd 2005); however, seed germination and establishment of *Heliconia acuminata*, an herbaceous perennial plant, are negatively affected by fragmentation, resulting in reductions of recruitment (Bruna 2002, 2003). Researchers have also reported that plant density has no effect on reproductive success, but habitat fragmentation and isolation have a negative effect on the reproductive success of *Cestrum parqui* (Solanaceae), as plants in small isolated populations were more likely to be pollination or pollen-limited than plants in larger populations (Aizen and Feinsinger 1994; Aguilar and Galetto 2004; Aguilar *et al.* 2006). *Angadenia berteroi*, predominantly self-incompatible and relying on pollinators for reproductive success (Barrios and Koptur 2011), was expected to reveal the adverse impact of fragment size and number of

adults on reproductive success. In our SEM results that confirm agreement between hypothetical and empirical models, a lack of strong direct effects of either fragmentation or number of adults on reproductive success simply emphasizes the importance of other factors related to habitat conditions for reproductive success of this species in fire-adapted pine rocklands.

Our SEM results also indicated that low canopy cover increases reproductive output of *A. berteroi* (Fig. 1). Yates and Ladd (2005) reported similar results, with increased reproduction and germination of *Verticordia fimbriolepis* on roadsides or in disturbed areas with little plant cover. Harrod and Halpern (2009) reported that flowering appears to be stimulated by increased light availability and low litter cover resulting from recent fires. In the case of *A. berteroi* also, previous work suggested that greater light availability has a positive impact on its reproductive success of *A. berteroi* (Barrios *et al.* 2011). Thus, the SEM results showing the direct significant effect of subcanopy cover on both reproductive success and seedling density corroborates earlier findings (Barrios *et al.* 2011), emphasizing the importance of low subcanopy cover for maintaining a healthy population of native species like *A. berteroi* in pine rocklands.

The effects of habitat fragmentation on seed germination and seedling fitness remain unclear. However, our results are in concordance with observations of Eisto *et al.* (2000) who reported that population size in the perennial herb *Campanula cervicaria* had no effect on its seed germination. These results were surprising since plants in small populations may have reduced fitness due to the effects of inbreeding depression and lower genetic diversity caused by fragmentation (Honnay and Jacquemyn 2007). The seed germination and seedling fitness of the *A. berteroi* populations sampled in this study may not have been affected by fragmentation, either because the fragments were large enough to maintain the minimum critical population size, or the fragments were not completely isolated from other sites, thus allowing seed and/or pollen dispersal between fragments.

The major finding of this study is the strong negative effect of habitat quality, rather than fragment area or plant density, on the reproductive success and seedling abundance of *A. berteroi*. Hobbs and Yates (2003) and McKechnie and Sargent (2013) found that altered local environmental conditions within remaining habitat can significantly alter the growth rate and reproduction of plant species. In addition to fragment quality, connectivity and landscape characteristics in which the habitats are embedded may also influence population survival and reproduction (Tscharntke and Brandl 2004). The habitat of *A. berteroi* has suffered from severe anthropogenic disturbance, both urbanization and agricultural intensification in recent decades (Snyder *et al.* 1990). The surrounding matrix (both agricultural or sand urban) may change habitat conditions in the fragments, affecting pollinator diversity and composition (Ahrne *et al.* 2009; Frankie *et al.* 2009; Carre *et al.* 2009), thus affecting

the reproductive success of the plants in the remaining fragments (Aguilar *et al.* 2006; Ferreira 2013; Newman *et al.* 2013).

In summary, although habitat fragmentation did not have a direct and great impact on reproductive success of *A. berteroi*, litter depth and subcanopy cover had strong negative effects on both its reproductive success and fitness. Since both litter depth and subcanopy cover in pine forests are a function of time since the last fire, we suggest that the increased light availability and low litter cover resulting from periodic fires favor reproduction of this native species of the southern Florida pine rocklands. These results emphasize the importance of fire as a tool for the habitat management and the conservation of this and other endemic species.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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